Ripples in the Anterior Auditory Field and Inferior Colliculus of the Ferret

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Supported in part by the Air Force Office of Scientific Research, the Office of Naval Research, the National Science Foundation Grant CD-8803012 and the National Institutes of Health.
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The original document contains color images.
Methods

- Responses of single units in AI, anterior field (AAF), and Inferior Colliculus (IC) in the barbiturate-anaesthetized ferret were recorded with single tungsten electrodes. Data were collected from a total of 7, 5 and 11 (resp.) ferrets, each weighing between 1.5 - 2.1 kg.

- Surgery and Animal Preparation: The techniques involved in the surgery and preparation for recording are described in detail in Shamma et al. (1993). The ferrets were anesthetized with pentobarbital sodium (40 mg/kg IP) and maintained in an areflexic state using a continuous IV infusion of pentobarbital (~ 5 mg/kg/hr) diluted with dextrose-electrolyte solution for metabolic stability. Data collection typically lasted 60-70 hours.

- Recording Procedures: Single-unit action potentials were recorded using glass-insulated tungsten microelectrodes with 5 to 6 MΩ impedances. The recorded signals were led through amplifiers and filters. Depending on the paradigm, a stimulus was presented every few seconds, and raster plots with 1ms time resolution were produced.

- In AI, recordings were typically made at depths of 300 - 600 µm (layers III and IV). In AAF, electrode penetrations were made parallel to the depth of the suprasylvian sulcus (SSS), approximately 0.5 mm caudal of the sulcus so that cortical layers III and/or IV were reached. IC was exposed by removal of (visual) cortex, and electrodes were lowered until ICC was reached, following standard criteria.
Change in Ripple Phase

\[ \Omega = 1.0 \text{ cyc/oct} \]

Phase (degrees)

Amplitude

Tonotopic Axis
Measuring the Ripple Transfer Function

Tonotopic Axis

Ripple Frequency (cyc/oct)

-1 0 1 2 3 4 5

0 0.4 0.8 1.2 1.6 2

Phase

0 0.5 1

Amplitude

0 0.5 1

Ripple Frequency (cyc/oct)

0 0.4 0.8 1.2 1.6 2

0 0.5 1

1.0 cyc/oct

0.4 cyc/oct

0.0 cyc/oct

Phase

0 0.5 1

0 0.5 1
0.8 cycles/octave at 8 different phases

Stimulus onset: 100 ms
Stimulus offset: 150 ms

0 phase ripple at 6 different ripple freq.
Tuning as a function of Ripple Frequency and Phase

### Graphs

- **Amplitude vs. Ripple Frequency (cyc/ct)**: The amplitude increases with the ripple frequency, reaching a peak around 1 cycle/octave and then decreases.

- **Phase vs. Ripple Frequency (radians)**: The phase decreases linearly with the ripple frequency, indicating a phase shift that increases as the frequency increases.

### Table

<table>
<thead>
<tr>
<th>Ripple Frequency (cyc/ct)</th>
<th>Intensity (dB)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>0.40</td>
<td>0.40</td>
</tr>
<tr>
<td>0.80</td>
<td>0.80</td>
</tr>
<tr>
<td>1.20</td>
<td>1.20</td>
</tr>
<tr>
<td>1.60</td>
<td>1.60</td>
</tr>
<tr>
<td>2.00</td>
<td>2.00</td>
</tr>
</tbody>
</table>

### Ripple Phase (degrees)

- 0°: No ripple
- 45°: 45° ripple
- 90°: 90° ripple
- 135°: 135° ripple
- 180°: 180° ripple
- 225°: 225° ripple
- 270°: 270° ripple
- 315°: 315° ripple
Response fields of varying bandwidth

| $|T(\Omega)|$ | $\Phi(\Omega)$ | RF |
|----------------|----------------|-----|
| ![Graph A](image1) | ![Graph B](image2) | ![Graph C](image3) |

- $\Omega_o = 0.6$
- $\phi_o = -10^\circ$
- $BF_{RF} = 5.2$ kHz

- $\Omega_o = 2.0$
- $\phi_o = -11^\circ$
- $BF_{RF} = 5.9$ kHz

- Frequency (kHz): 0.0 0.8 1.6 2.4 3.2 4.0
- Spike Count: 0 1 2 3 4 5 6 7 8
- $\Omega$ (cycles/octave): 0.0 0.8 1.6 2.4 3.2 4.0
- $\phi$ (radians): $-2\pi$ $-4\pi$ $-6\pi$ $-8\pi$ $-10\pi$

15701a
15206d
Response Fields with varying asymmetries

A

$|T(Ω)|$

$Ω_0 = 0.8$

Spike Count

$Δ (Ω)$

$Φ (Ω)$

$ϕ_0 = -106°$

Spike Count

RF

$BF_{RF} = 9.4$ kHz

B

$Ω_0 = 0.8$

$ϕ_0 = 42°$

$BF_{RF} = 7.6$ kHz
The Anterior Cortical Field
BF’s and latencies are similar

- **N = 147**
  - AAF

- **N = 168**
  - AI

- **N = 139**
  - AAF

- **N = 165**
  - AI
Bandwidths (BW20) are larger in AAF

N = 128

N = 151

AAF

AI
Tuning to Ripples tends to be lower in AAF

RF’s asymmetries are evenly distributed
Predictions Using Stationary Ripples

Response Field of Cell

Spectral Profile of stimulus

Response of Cell to Profile

Measured Response
Predicted Response
Response to flat spectrum
The Inferior Colliculus
Of BF’s and Latencies

N = 138
IC

N = 168
AI

N = 140
IC

N = 165
AI
Bandwidths

\[ N = 138 \]
\[ N = 151 \]

\[ \text{IC} \]
\[ \text{AI} \]
$\Omega_0 = \text{Best Ripple Frequency}$

- **AI**: N = 155
- **IC**: N = 140
- **IC**: N = 53

Tuning at .2 (c/0) / Tuning at best ripple
RF’s are more symmetrical in IC

- IC: N = 138
- AI: N = 155

Histograms show the distribution of counts for different angles (Phi) with bars representing single units and shaded bars representing clusters.
Temporal properties: Moving Ripples

- $\Omega = \text{ripple frequency in cycle/octaves}$
- $\omega = \text{temporal frequency in Hz}$

$\omega = 4 \text{ Hz}$

$t = 0 \text{ ms}$

$t = 62.5 \text{ ms}$

$t = 125 \text{ ms}$

$t = 187.5 \text{ ms}$

Tonotopic Axis (kHz)

Tonotopic Axis

Response Field of Cell

Expected Response

$\tau_d$ $\tau_m$

$t$
Responses to Moving Ripples

Ripple Frequency is 0.4 cycles/oct

$\Omega = 0.4 \text{ cyc/oct}$

$\omega = 4 \text{ to } 32 \text{ Hz}$

30 sweeps per $\omega$
Step 1. From Spike Count to Period Histogram

Step 2. Magnitude and Phase of Best Fit

\[ |T_{\Omega_b}(\omega)| \]

\[ \Phi_{\Omega_b}(\omega) \]

\[ \hat{\Phi}_{\Omega_b}(\omega) \rightarrow \Phi_{\Omega_b}(0) \]

\[ F^{-1} \]

\[ IR(t) \]
Linearity of responses in the Auditory Cortex

AI and AAF display similar characteristics

Anterior Field:

(A) Stimulus Spectrogram, $S(x,t)$  (B) $RF(x)$  (C) $\sum RF(x) \cdot S(x,t)$  (D) $IR(t)$  (E) Predicted Response
Predicting the Response to a Complex Stimulus

Primary Auditory Cortex:

(A) Stimulus Spectrogram, $S(x,t)$
(B) $RF(x)$
(C) $\sum RF(x) \cdot S(x,t)$
(D) $IR(t)$
(E) Predicted Response

4+8 Hz at 0.4 cyc/ oct

$\rho = .74$

4+8+12+16 Hz at 1.2 cyc/ oct

$\rho = .94$
$\Omega = 0.2$ cyc/oct

Temporal Frequency (Hz)

$\omega = 4$ to 64 Hz

Ripple Frequency is 0.2 cyc/oct

Inferior Colliculus Responses

15 sweeps per $\omega$
Summary

- Stationary and traveling ripples can be used to extract spectral and temporal properties of auditory cortical neurons.
- Linearity: Responses to a broad-band complex stimuli, decomposed into a linear combination of ripples, can be predicted by summing the neuronal responses to the individual ripples.
- Only Cortical neurons are selective to ripple frequencies; Collicular neurons are low-pass with respect to ripple frequencies.
- Therefore, AI and AAF neurons could perform a multi-scale analysis of spectral shape: the spectral profile is analyzed at different degrees of resolution by neurons with receptive fields of different best frequencies, bandwidths and asymmetries.
References

- Owens A. and Shamma S. “Surface evoked potentials reveal selectivity to spectral shape features”. ARO 96.
